

STUDIES ON DEROPRISTIS INFLATA (MOLIN), ITS LIFE HISTORY AND AFFINITIES TO TREMATODES OF THE FAMILY ACANTHOCOLPIDAE

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INTRODUCTION

During the summer of 1939, three undescribed species of cercariae, one of which was a modified trichocercous larva, were found in the marine snail, *Bittium alternatum*, from Waquoit Bay, Cape Cod, Massachusetts. This trichocercous cercaria penetrated and encysted in *Nereis virens* and this annelid, when collected in the vicinity of infected snails, was found to be naturally infected. Of the trematodes that had been found in an extended survey of fish parasites in the vicinity, only two species could be regarded as possibly the adult of the cercaria in question; these were *Deropristis inflata*, belonging to the family Acanthocolpidae, and *Homalometron pallidum*, a species allocated to the subfamily Anallocreadiinae, family Allocreadiidae. Of the two, *H. pallidum* was at first believed most likely to be the adult of the cercaria from *B. alternatum*, since Hopkins (1937) had described remarkably similar cercariae for *Anallocreadium* and *Microcreadium*, both anallocreadiine genera closely related to *Homalometron*. This belief was supported by a comparison of the present cercaria with the adult of *H. pallidum* which showed that they agreed in possessing eye-spot pigment, a short, sac-shaped excretory vesicle, ciliated main excretory tubules reaching only to the ventral sucker, and similar branching of secondary tubules.

Each new life history study provides increasing evidence that trematodes properly allocated to the same family have life cycles involving similar embryological and larval stages and usually intermediate hosts that are closely related. It seemed unlikely, therefore, that *D. inflata*, a member of the family Acanthocolpidae, would have a trichocercous cercaria that encysted in annelids, since Martin (1939) had shown that another acanthocolpid, *Stephanostomum tenue*, has an ophthalmoxiophidio-cercariae which encysts in fishes. Furthermore, metacercariae of at least

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two other genera in the family are known to occur in fishes. Although Carrère (1937, 1938) had identified a metacercaria from *Nereis dumerilli* as that of *D. inflata*, his observations did not seem at first to be significant for the present study since a number of cercariae encyst in species of *Nereis* and the most variable phase of the trematode cycle is that enabling the parasite to reach the definitive host. Feeding experiments, however, have demonstrated conclusively that the cercaria from *B. alternatum* is that of *D. inflata* and that the family Acanthocolpidae, as constituted at present, is not a natural group of closely related trematodes.

Although numerous species have been described and allocated to certain acanthocolpid genera, particularly *Stephanostomum* (here regarded as taking precedence over *Stephanochasmus* in accordance with the recommendation in Article 36 of the Rules of Nomenclature), a critical analysis of the family has been prevented by a lack of information concerning the type genus *Acanthocolpus*, and particularly the excretory system and life histories of acanthocolpids. The imperfectly described *Acanthocolpus liodorus* was the only known representative of the type genus until Srivastava (1939) described three new species of *Acanthocolpus* from Indian marine fishes. A better understanding of the type genus, and knowledge of the life histories and excretory systems of *Stephanostomum tenue* and *Deropristis inflata*, afford an opportunity to analyze the interrelationships of the acanthocolpid trematodes and their affinities to other groups.

HISTORICAL REVIEW

Ward (1938) has reviewed the family Acanthocolpidae and the genus *Deropristis*, supplementing previous descriptions of the two known species, *D. inflata* (Molin) and *D. hispida* (Albildgaard). References concerning these species may be obtained from Ward's paper and need not be repeated here. A brief review of the family is desirable as a basis for discussion later.

The first attempt to group the trematodes at present allocated to the family Acanthocolpidae was made by Lühe (1906) who proposed the subfamily Acanthocolpinae (family unmentioned) to contain the genera *Acanthocolpus*, *Stephanochasmus* (syn. *Stephanostomum*), and *Deropristis*, and the species *Distomum semiarmatum* Molin. Later, Lühe (1909) established the family Acanthocolpidae, apparently to contain all these forms although he mentioned only *Deropristis inflata*, *D. hispida*, and *Distomum semiarmatum*; these species occur in migratory fishes and Lühe was concerned with only freshwater forms. He did not propose a subfamily Acanthocolpinae at that time, as assumed by some authors,

but stated that the various genera apparently belonged to several sub-families. Odhner (1911), evidently disregarding Lühe's proposal, stated that *Stephanochasmus*, *Dihemistephanus*, *Acanthopsolus*, and *Distomum osculatum* Looss constituted a distinct family but did not propose a name for it. Nicoll (1913) erected the genus *Lepidauchen* which seemed to him to be an intermediate form combining the characters of the genera *Lepocreadium* and *Stephanochasmus*. He later (1915) placed *Lepidauchen* in the Lepocreadiinae, *Stephanochasmus* and *Acanthopsolus* in the Stephanochasminae, all of the family Allocreadiidae, and *Deropristis* in a list of forms of uncertain position. Poche (1925) criticized Nicoll's allocation of *Stephanochasmus* and *Acanthopsolus* to the family Allocreadiidae, removing these genera to the family Acanthocolpidae, to which he added *Dihemistephanus*, *Acanthopsolus*, and the new genus *Tormopsolus*. He also followed Pratt (1916) in reducing *Lechradena* to synonymy with *Stephanochasmus* and Odhner (1911) in the opinion that *Neophasis* is synonymous with *Acanthopsolus*. To include a new genus, *Echinostephanus*, Yamaguti (1934) redefined the subfamily Stephanochasminae, placing it in the family Acanthocolpidae. Ward (1938) denied the validity of both the genus *Echinostephanus* and the subfamily Stephanochasminae, but proposed a new subfamily, Acanthopsolinae, for the single genus *Acanthopsolus*.

MATERIALS AND METHODS

During the summers 1939-41, several thousand *Bittium alternatum* were examined for larval trematodes. The snails were collected from Waquoit Bay at Menauhant, Massachusetts, and the infected specimens were separated by isolation to provide an abundant supply of cercariae. To obtain metacercariae of known age, a specimen of *Nereis* was placed in a large crystallizing dish and exposed to all the cercariae that emerged from a number of infected snails during a 24-hour period. After exposure, each annelid was kept either in a finger bowl half filled with sand, covered with cheesecloth, and placed in running sea water, or in a dish of water which was aerated without changing. Various species of fish for feeding experiments were isolated in the laboratory for at least three weeks before use. The experimental animals were killed and examined from one to seven days after being fed infected annelids. If, kept for longer periods, the worms either failed to establish themselves in unsuitable hosts such as *Fundulus* and flounders, or the eel, the natural host, they developed until they could not be distinguished with certainty from worms that might have been present when the fish was collected.

Throughout the study, living material was used extensively although

measurements were taken mostly from recently killed or fixed and stained specimens. Since the living cercaria is extremely active and difficult to measure without considerable coverglass pressure, measurements were taken mostly from larvae that were killed by placing them on a slide in a large drop of water, covering and holding over a flame for a moment. When treated in this manner, practically every cercaria died in a moderately extended, straightened position, and the body did not become opaque as when killed with the usual fixatives.

Neutral red and Nile blue sulfate were used supravitaly and permanent whole mounts were stained with paracarmine. All measurements are in millimeters and all figures, except those indicated as free-hand drawings, were made with the aid of a camera lucida.

We wish to express our thanks to Dr. H. W. Manter for the privilege of examining material of *Dihemistephanus brachyderus* and to Professor H. W. Stunkard for helpful suggestions and criticism during the preparation of the manuscript.

OBSERVATIONS

Proof of the Life History of Deropristis inflata

Since at first we suspected that the cercaria was the larva of *Homalometron pallidum*, both naturally and experimentally infected annelids were fed to four *Fundulus heteroclitus*, a species which serves as the natural host of that trematode. These fish were examined five days later and found to be uninfected. Next, a large *Nereis*, heavily infected with 14-day metacercariae, was fed to a summer flounder, *Paralichthys dentatus*, which had been isolated for four weeks and had begun to take food. When killed and examined the following day, several hundred recently excysted worms were recovered from the intestine. These worms were all the same size and showed the conspicuous spines of the dorsal hump and lateral forebody characteristic of *Deropristis*. This observation was made too late to conduct further experiments until the following summer (1941) when the study was continued and the feeding of experimentally infected annelids to eels yielded large numbers of immature *Deropristis*. Control fish were either negative for *D. inflata* or harbored only specimens in an advanced stage of development. A careful study of the metacercaria revealed that the peculiar spination of *Deropristis* was just beginning to differentiate, the dorsal and lateral spines being distinctly larger than adjacent body spines.

Finally, a careful comparison of the excretory system of the cercaria and that of the young adult in both natural and experimental infections showed complete agreement. Thus the experimental results

and morphological evidence afford conclusive proof of the life history of *D. inflata*.

Description of stages in the life history of Deropristis inflata
Adult (Figs. 1-5)

The common eel, *Anguilla rostrata*, serves as the natural definitive host of *D. inflata* in the Woods Hole region. Practically every eel examined, except those that had been in captivity for several weeks, was found to be infected. The worms occurred throughout the intestine, being more numerous toward its posterior end.

The fairly complete accounts given by Odhner (1902) and Linton (1940) and supplementary observations by Manter (1926) and Ward (1938) make it unnecessary to give a complete redescription of *D. inflata*. Measurements of our specimens are well within the limits given in other descriptions. General morphological features are shown in Figs. 1-4. Since extensive observations have been made on living specimens, it is desirable to supplement existing descriptions of body spination and the reproductive and excretory systems.

EXPLANATION OF PLATE I

(All figures concern *Deropristis inflata*)

- FIG. 1. Mature adult, ventral aspect.
FIG. 2. Spines of (A) metraterm and (B) cirrus (free-hand).
FIG. 3. Adult. Dorsal aspect of anterior end showing details of spination (many small spines omitted).
FIG. 4. Adult. Lateral view showing details of spination and terminal genitalia (many small spines omitted).
FIG. 5. Female reproductive system, dorsal view (free-hand).
FIG. 6. Embryonated egg from terminal portion of uterus.

ABBREVIATIONS

<i>CI</i> , cirrus.	<i>OS</i> , oral sucker.
<i>CS</i> , cirrus sac.	<i>OT</i> , oötype.
<i>DV</i> , common vitelline duct.	<i>OV</i> , ovary.
<i>EG</i> , egg.	<i>PH</i> , pharynx.
<i>EP</i> , excretory pore.	<i>PR</i> , prostate cells.
<i>ES</i> , esophagus.	<i>RV</i> , right vas efferens.
<i>EV</i> , excretory vesicle.	<i>SC</i> , cervical spines.
<i>EY</i> , eye-spot pigment.	<i>SD</i> , dorsal hump spines.
<i>GA</i> , genital atrium or sinus.	<i>SR</i> , seminal receptacle.
<i>GL</i> , cervical gland.	<i>SV</i> , seminal vesicle.
<i>GP</i> , genital pore.	<i>TE</i> , testes.
<i>IN</i> , intestine.	<i>TV</i> , transverse vitelline duct.
<i>LC</i> , Laurer's canal.	<i>UT</i> , uterus.
<i>LV</i> , left vas efferens.	<i>VD</i> , vas deferens.
<i>ME</i> , metraterm.	<i>VI</i> , vitellaria.
<i>MG</i> , Mehlis' gland.	<i>VR</i> , vitelline reservoir.
<i>OD</i> , oviduct.	<i>VS</i> , ventral sucker.

Although spination of the body has been described rather fully, certain features have apparently been overlooked. The first three rows of spines behind the ventral lip of the oral sucker are slightly larger than those posterior to this level and the concave ventral surface of the body is devoid of spines from about the level of the cervical expansions to the ventral sucker. The large spines of the dorsal hump (Fig. 3) and probably also those of the cervical expansions (Fig. 4) develop at first as members of rows of spines quincuncially arranged. The number of enlarged spines on the dorsal hump is variable, but in very young worms there are usually ten in transverse rows of three, four and three. Adjacent spines are more or less enlarged in mature worms and the large spines become very prominent, more or less masking the original quincuncial pattern. They may become worn with age or even lost, giving the dorsal hump a ragged appearance. In living specimens, numerous conspicuous glands in the forebody are seen to open among the prominent spines of the cervical expansions. The ducts of a few such glands also open on the ventral surface of the forebody.

Living *D. inflata* is extremely favorable material for observing the reproductive system, the details of which can be observed completely in almost every specimen. The oviduct (Fig. 5) extends from the right side of the ovary for a short distance and then turns dorsally and to the left where its junction with the duct of the seminal receptacle, Laurer's canal, and the oötype forms a cross. From this junction, Laurer's canal extends to the left, opening at the dorsal surface considerably to the left of the median line. The oötype extends forward a short distance and then turns to the right, immediately receiving the duct of the vitelline reservoir. Just beyond this point, the oötype is surrounded by a moderately developed Mehlis' gland. From the oötype, the uterus extends posteriorly to the right of the ovary and returns on the same side. In young worms, this posterior loop does not extend behind the ovary while in large, mature specimens, it may form convolutions between the female complex and the anterior testis. In front of the ovary, the uterus extends anteriorly as a moderately sinuous tube and joins the prominent metraterm with its conspicuous lining of spines. The vitelline follicles are diffuse and confined to the region between the cirrus and the anterior testis. The transverse vitelline ducts, which unite to form the vitelline reservoir, are ventral to the remainder of the female complex.

In large worms, the eggs are fairly numerous, and in fresh material measure from 0.042 to 0.052 mm. long and 0.024 to 0.026 mm. wide. They are fairly thick-shelled and operculate; older ones are brown in color and contain active embryos, but eggs teased from worms and kept for ten days in sea water failed to hatch.

The testes (Fig. 1) lie near the posterior end of the body, one behind the other or slightly overlapping. The vas efferens of the anterior testis is to the left of the median line while that of the posterior testis is to the right. The left vas efferens passes between Laurer's canal and the vitelline duct of that side, while the right runs through the loop of the oviduct. Anterior to the female complex, the vasa efferentia unite to form the vas deferens which is about as long as the seminal vesicle and slightly enlarged posteriorly. The cirrus sac is longer than the metraterm and contains the seminal vesicle, pars prostatica, and prominent, spined cirrus. A short distance posterior to the ventral sucker, the metraterm and cirrus sac join the slender, tubular genital sinus. The largest spines of the metraterm and cirrus (Fig. 2) are about 0.04 mm. long, and of similar structure, but slightly different in shape, those of the metraterm being a little wider. Each spine consists of an acute, refractile point and a very delicate, hyaline medullary and basal portion, and is very different from the body spines in structure, as noted by Olsson (1867) and Ward (1938). In one aberrant specimen, spines similar to those of the metraterm were observed in the genital sinus.

The excretory system (Fig. 11) has been completely traced in young worms obtained from both naturally and experimentally infected eels. The excretory pore is at the posterior end of the body. The vesicle is sac-shaped and extends anteriorly as far as the anterior testis. The main excretory tubules are ciliated throughout their length and extend from the anterolateral edges of the vesicle almost to the ventral sucker where each receives an anterior and a posterior collecting tubule. Each of these tubules serves three groups of flame cells but the disposition of secondary tubules and numbers of flame cells in the groups are not the same for anterior and posterior halves of the system. These differences may be noted in Fig. 11. There may be five, six, or even more flame cells in the posterior-most group on each side, depending on the size of the worm. One flame cell of this group is larger than the others and has a more conspicuous capillary which joins the collecting tubule separately from and anterior to the capillaries of the remaining flame cells of the posterior group. There is also a marked lack of dichotomy in the arrangement of the capillaries in other flame cell groups. The excretory formula of fairly young adults is $2[(3 + 5 + 7) + (4 + 4 + 6)] = 58$ flame cells. There is an increase in the number of flame cells during post-cercarial development but only in the groups associated with the posterior collecting tubules.

The Cercaria (Figs. 7-8)

Specific Diagnosis.—Distome modified trichocercous type. Body pyriform in shape with maximum width anterior to ventral sucker; spi-

nose anterior to eye-spots; extended length over 0.4, contracted less than 0.13. Tail extended 0.33, contracted 0.19. Measurements of 10 cercariae killed by heat: body length 0.21–.28 (average 0.25); maximum width 0.08–.1 (0.086); length of tail 0.2–.23 (0.21), width near base 0.026–.03 (0.028); oral sucker diameter 0.04–.045 (0.043); ventral sucker 0.043–.045 (0.044), situated in posterior half of body; average length of prepharynx 0.023, pharynx 0.017; eye-spots 0.011 wide. Tail typically with a ventral fin-fold and 6 pairs of ventrolateral tubercles, each with a long delicate “hair.” Prepharynx moderately long, pharynx present, intestinal ceca extending almost to posterior end of body. At least eight pairs of cephalic glands anterior to ventral sucker; numerous gland-like cells and refractile droplets throughout body. Genital primordium an undifferentiated mass posterior to ventral sucker. Excretory vesicle sac-shaped, thick-walled and with numerous concretions. Main excretory tubules ciliated. Flame cell formula $2[(3 + 5 + 7) + (3 + 3 + 5)] = 52$ flame cells. Develop in rediae in the branchial region and digestive gland of the molluscan host.

Host: Bittium alternatum (Say).

Locality—Waquoit Bay, Falmouth, Massachusetts, U. S. A.

Study of the excretory system of the cercaria in the light of observations on the adult stage necessitates correcting our preliminary abstract (Cable and Hunninen, 1940). The excretory formula of the cercaria, as included in the above specific diagnosis, is not in agreement with that given in the abstract. The flame cells and capillaries of the cercaria are extremely small and the presence of numerous glands and refractile droplets makes it very difficult to observe details of the excretory system.

EXPLANATION OF PLATE II

(All figures concern *Deropristis inflata*)

FIG. 7. Cercaria, ventral aspect.

FIG. 8. Cercaria, median sagittal (optical) section of anterior end showing papilla resembling stylet (free-hand).

FIG. 9. Redia, showing excretory system of one side (free-hand).

FIG. 10. Five-day metacercaria.

FIG. 11. Excretory system of young adult (free-hand).

ABBREVIATIONS

CG, cephalic glands.
CT, caudal tubercle.
EC, excretory concretion.
EP, excretory pore.
EV, excretory vesicle.
EY, eye-spot.
GD, cephalic gland ducts.
IN, intestine.

OS, oral sucker.
PG, genital primordium.
PH, pharynx.
PP, prepharynx.
PS, stylet-like papilla.
RD, refractile droplets.
VF, ventral fin-fold.
VS, ventral sucker.

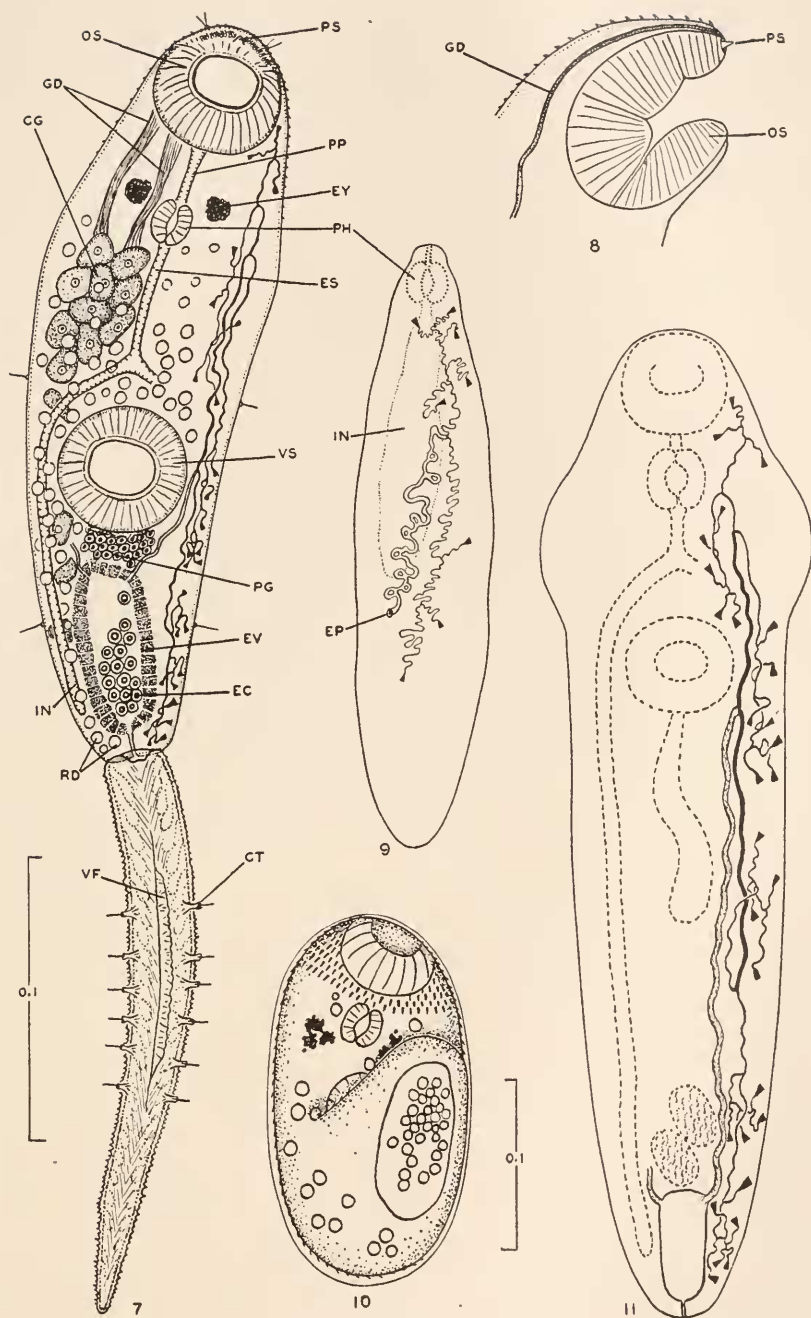


PLATE II

For several hours after emerging from the snail, the cercariae of *D. inflata* swim almost continuously, tail first, lashing in a figure eight, with the body flexed so that the anterior end is pointed in the direction of swimming. When dissected from the snail, they are photopositive but naturally emerging cercariae are decidedly photonegative and collect at the side of the dish farthest from the light. Precisely the same behavior has been described by Hopkins (1937) for the cercariae of *Anallocreadium* and *Microcreadium*. In one set of experiments with alternate illumination of opposite sides of a syracuse dish, it was observed that when the direction of the light was reversed, the cercariae would swim as a rather compact group across the dish in less than one minute. By illuminating both sides of the dish at once, the larvae scattered; swimming in a hesitant manner. In many cases, decaudation was noted after which the cercarial body remained alive for several hours.

The body of the cercaria is widest apparently at the level where the prominent cervical expansions will develop later. It tapers posteriorly and is devoid of general pigmentation. The eye-spots are conspicuous and contain a refractile body. When contracted the tail is almost as wide as the posterior end of the body and has finely crenated edges. The fin-fold is narrow and crinkled. Although the tail typically has six tubercles symmetrically arranged along each side, there is considerable variation in the number, size, and arrangement of these structures. Accessory tubercles may be present and one specimen was observed in which they were seen on only one side of the tail.

The dorsal lip of the oral sucker bears a blunt, papilla-like structure (Fig. 8) which is difficult to interpret. It is about 0.004 mm. long, conical, non-refractile, and set in what appears to be a slight depression. This structure was first regarded as possibly a rudimentary stylet. However, it is directed anteriorly rather than dorsally as in "allocreadiid" cercariae and has more the appearance of a papilla; the ducts of the cephalic glands do not converge toward it but instead open in a row along the dorsal lip of the oral sucker. We are therefore inclined to believe that the structure in question is not homologous with the stylet of other cercariae. Consequently, we can see no reason to postulate that the cercaria of *D. inflata* is an intermediate type between the ophthalmoxiphidiocercariae and trichocercous forms.

Of the described species of trichocercous larvae, the cercaria of *D. inflata* most closely resembles the cercariae of *Anallocreadium* and *Microcreadium* as described by Hopkins (1937). In fact, it was this resemblance that first led us to suspect that *Homalometron pallidum* might be the adult stage of the larva we were studying. A comparison of the cercariae of *Anallocreadium*, *Microcreadium*, *Deropristis*, and *Stepha-*

nostomum will be given in connection with an analysis of the family Acanthocolpidae in the discussion.

The Redia (Fig. 9)

Two redial generations were observed. The simple elongate daughter redia attains a length of over 1 mm. In living specimens, the pharynx measures 0.045 mm. in diameter and is followed by a short, expanded intestine with orange-yellow contents. There is a birth pore near the pharynx. Cercariae reach apparently complete development in the redia which may contain as many as 14 active larvae. In addition to cercariae, even the largest redia contains a group of germ cells situated at the posterior end of the brood cavity.

There is a striking homology between the excretory system (Fig. 9) of the daughter redia and that of the cercaria. Not only are the main excretory tubules ciliated in both stages, but the branching of the tubules and the number of flame cell groups are essentially the same, although with the exception of the anterior-most, the flame cell groups of the cercaria and adult are represented in the redia by single flame cells. As compared with the adult, then, the daughter redia has the complete flame cell complement in only the anterior-most group while the cercaria has the adult complement in three groups or all those connected with the anterior collecting tubule. While we have not had favorable material for determining the excretory patterns of the miracidium and mother redia, the above observations afford convincing evidence of recapitulation in the development of the excretory system in the various life history stages.

The Metacercaria

When annelids were exposed to large numbers of cercariae, massive infections were obtained. The larvae encyst mostly in the axial body region of *Nereis*, although in heavy infections, they occur to a less extent in the parapodia. The cyst is oval in shape, and the primary cyst membrane is thin, and difficult to remove from the worms without injuring them. In older metacercariae, the cysts may become brown in color, particularly when localized in the parapodia. Ten living 5-day metacercariae (Fig. 10) measured 0.17–.23 mm. long and 0.11–.14 mm. wide. The metacercaria does not increase appreciably in size with age although a certain amount of development occurs. Five days after encystment, the sharp-pointed body spines, characteristic of the adult, are present well behind the ventral sucker and those which later become very prominent on the dorsal hump and at the sides of the forebody are just detectably larger than the remaining body spines. Also at this age, the

eye-spots begin to dissociate and the concretions of the excretory vesicle have more the appearance of oil droplets than in the cercaria.

DISCUSSION

The results of the present study and a review of the literature demonstrate certain fundamental differences between *Deropristis* and other genera heretofore allocated to the family Acanthocolpidae. A redefinition of the family will be helpful in summarizing these differences.

Family Acanthocolpidae Lühc, 1909, emend.

Oval or elongate distomes, body weakly muscular, oval to round in cross-section. Cuticle spinose, frequently with large spines associated with oral sucker. Remnants of cercarial eye-spots often present. Suckers relatively close together. Prepharynx usually long, pharynx well developed, esophagus short; intestinal ceca extend almost to posterior end of body, rarely joining the excretory vesicle or with diverticula. Excretory vesicle tubular, not reaching ventral sucker, and with a pair of main excretory tubules extending from its anterior end to cephalic region of body before receiving secondary tubules. Genital pore median or submedian, immediately anterior to ventral sucker or rarely opening within ventral sucker; genital atrium usually tubular, posterior portion sometimes with spines; cirrus sac present, metraterm and cirrus often with prominent spines. Testes two (rarely multiple), in posterior region of body, tandem or obliquely one in front of the other; ovary near or some distance in front of anterior testis; seminal receptacle lacking, uterine seminal receptacle frequently present; vitelline follicles numerous, reaching from level of cirrus sac to posterior end of body. Uterine coils preovarian and intercecal, not extensive; eggs relatively few, operculate and without filaments. Adults parasitic in intestine of marine fishes, metacercariae in fishes. Cercaria of ophthamoxiphidiocercous type, developing in simple rediae in marine gastropods. Type genus, *Acanthocolpus* Lühc, 1906. Includes also:

Stephanostomum Looss, 1899 (syn. *Stephanochasmus* Looss, 1900;

Lechradena Linton, 1910).

Dihemistephanus Looss, 1901.

Neophasis Stafford, 1904 (syn. *Acanthopsolus* Odhner, 1905).

Tormopsolus Poche, 1925.

Echinostephanus Yamaguti, 1934.

Lepidauchen Nicoll, 1913.

Pleorchis Railliet, 1896 (syn. *Polyorchis* Stossich, 1888, preoccupied).

Pseudolepidapedon Yamaguti, 1938.

A careful comparison of the above genera indicates a sufficiently close interrelationship to preclude the necessity of subfamilies.

In contrast with the family Acanthocolpidae as set forth above, *Deropristis* has a modified trichocercous cercaria which encysts in annelids; the main excretory tubules barely reach the ventral sucker; there is a well developed seminal receptacle independent of Laurer's canal; vitelline follicles are scanty and restricted to the region between the cirrus sac and the anterior testis; the uterine coils extend into the space between the ovary and anterior testis; and the prepharynx is shorter than the esophagus. These differences fully justify the exclusion of the genus *Deropristis* from the Acanthocolpidae.

The above definition of the family excludes also the species described by Little (1930) as *Dihemistephanus sturionis*; it is very doubtful whether this form belongs in either the genus *Dihemistephanus* or the family Acanthocolpidae, since Laurer's canal is enlarged to form a seminal receptacle, the vitelline follicles as figured appear scanty and do not extend to the extreme posterior end of the body while the uterus does, and the eggs are small and numerous. Also, the cephalic spines apparently are not as closely associated with the oral sucker as in *D. lydiae* (Looss, 1901; Nicoll, 1909), being arranged more like those of the echinostome collar and lacking the two rows of smaller spines in the ventral gap.

Dihemistephanus brachyderus Manter, 1940, is in agreement with the family diagnosis in most respects although it has two ascending excretory tubules on each side formed by the division of each main tubule a short distance from the vesicle. We have examined a specimen of *D. brachyderus*, kindly provided by Professor Manter, and found that the female complex is typical of the Acanthocolpidae; a Laurer's canal is present and the beginning portion of the uterus is expanded to form a prominent receptaculum uterinum, a true seminal receptacle being absent. In all other respects except the ascending excretory tubules, which may represent an aberrant condition, *D. brachyderus* is typically acanthocolpid in structure, although its allocation to the genus *Dihemistephanus* is somewhat uncertain, as stated by Manter (1940). On the whole, however, *D. brachyderus* resembles *D. lydiae*, the type species, far more than does *D. sturionis*.

The descriptions of *Lepidauchen hysterospinosa* Manter, 1931, and *Pleorchis sciaenae* Yamaguti, 1938, extend our knowledge of genera hitherto imperfectly understood, so that they now may be included in the family Acanthocolpidae. Also, *Pseudolepidapedon* is unquestionably an acanthocolpid. *Lepidauchen* and *Pseudolepidapedon* differ from the

original genera of the family chiefly in respect to the terminal genitalia, a character whose taxonomic significance is often unreliable and has been greatly overestimated in proposing supergeneric groups. The presence of intestinal diverticula and multiple testes in *Pleorchis* are of not more than generic significance (compare *Fasciola* and *Fasciolopsis*; *Siphodera* and *Exorchis*). Since the genera *Pleorchis* and *Schistorchis*, for which Poche (1925) erected the family Pleorchiidae, do not seem to be at all closely related, this family must be judged invalid.

Although the acanthocolpids bear certain resemblances to the echinostomes, as noted by many authors, life history studies indicate that their closest relatives are to be sought among the allocreadiid trematodes having ophthalmoxiphidiocercariae. These include *Allocreadium*, *Crepidostomum*, *Megalogonia*, *Bunodera* and related genera. The family Allocreadiidae² should be restricted to include these forms. However, the acanthocolpids differ from the allocreadiids in morphology and host-parasite relationships. As far as known at present, allocreadiid cercariae develop in freshwater bivalves and encyst in invertebrates while acanthocolpid cercariae develop in marine gastropods and encyst in fishes. The chief morphological difference is in respect to the excretory system. In view of these differences, the Acanthocolpidae and Allocreadiidae are regarded for the present as distinct families of a common superfamily.

The systematic position of the genus *Deropristis* remains to be discussed. There seems no alternative to the conclusion that its nearest relatives are such forms as *Homalometron*, *Anallocreadium*, *Microcreadium* and *Lepocreadium*. In our opinion, the subfamilies Lepocreadiinae and Anallocreadiinae and the genus *Deropristis* constitute a family independent of the Allocreadiidae. As far as we have been able to determine, the only published proposal of such a combination is the grouping of several genera under the heading, Lepocreadiidae, in the Zoological Record for 1934. Since this list presumably is attributable to Nicoll, the sectional editor, the family is defined below under the following heading:

² The authors' (Hunninen and Cable, 1941) recent proposal to restrict the family Allocreadiidae to contain those trematodes having in common cotylomicrocerous cercariae and certain other characteristics was based on the assumption that *A. angusticollis* was actually a species of *Allocreadium* since it did not violate the original description of the genus. The description of *A. isoporum*, the type species, was unavailable at the time our paper was revised. This description fully justifies Dobrovolsky in transferring *A. angusticollis* to *Plagioporus*; although Looss performed no life history experiments with the ophthalmoxiphidiocercaria which he believed to be the larva of *A. isoporum*, it is very likely that his belief was correct. We therefore retract our proposal in favor of that of Hopkins (1941), viz., that the name Opcoelidae be used for the restricted family.

Lepocreadiidae Nicoll, 1934

Medium sized distomes, body variable in shape, rarely without spines. Mouth subterminal, prepharynx, pharynx, and esophagus present; intestinal ceca almost always long, rarely joining excretory vesicle or with separate anal openings. Excretory vesicle tubular, variable in length, frequently reaching pharyngeal level; rarely Y-shaped and then with short arms not receiving main tubules; excretory pore posterior, terminal or subterminal. Main excretory tubules never reach cephalic region but divide near acetabular level to form anterior and posterior collecting tubules. Flame cells numerous. Genital pore anterior to ventral sucker, median or displaced to left; rarely marginal or with a "genital sucker." Cirrus sac present or absent; if present almost always followed by an external seminal vesicle. Testes in posterior half of body, occasionally multiple, usually two, median and tandem, sometimes diagonal or opposite in short bodied forms. Ovary pretesticular, rarely behind level of anterior testis. True seminal receptacle and Laurer's canal present. Vitellaria usually extensive, often filling body posterior to ventral sucker, rarely confined between levels of cirrus sac and anterior testis or restricted to post-testicular region of body. Uterus preovarian in almost all genera and not extensive; eggs relatively few and large. Parasites of fishes. Cercariae of trichocercous type, stylet lacking, with conspicuous eye-spots remnants of which may persist in adults. Develop in simple rediae in gastropods, encyst in invertebrates. Includes the following subfamilies:

Lepocreadiinae Odhner, 1905

With characters of the family. Genital pore to left of median line; cirrus sac present, followed by external seminal vesicle which is sometimes embedded in a glandular mass. Vitellaria well developed, reaching posterior end of body; uterus preovarian in almost all genera. Parasites of marine fishes. Type genus *Lepocreadium* Stossich, 1903. Includes also:

Lepidapedon Stafford, 1904 (syn. *Lepodora* Odhner, 1905).

Opechona Looss, 1907 (syn. *Pharyngora* Lebour, 1908).

Aephniidiogenes Nicoll, 1915.

Pseudocreadium Layman, 1930 (syn. *Leptocreadium* Ozaki, 1936).

Diploporus Ozaki, 1928 (syn. *Bianium* Stunkard, 1930).

Multitestis Manter, 1931.

Rhagorchis Manter, 1931.

Lepotrema Ozaki, 1932.

Myzoxenus Manter, 1934.

Lepocreadioides Yamaguti, 1936.

Hypocreadium Ozaki, 1936.

Labrifer Yamaguti, 1940.

Allolepidapedon Yamaguti, 1940.

Opechonoides Yamaguti, 1940.

Homalometrinae nom. nov. pro *Anallocreadiinae* Hunter
and Bangham, 1932

With the characters of the family. Body not very elongate, with or without spines. Genital pore median, immediately in front of or rarely posterior to ventral sucker; cirrus sac lacking. Vitellaria well developed, rarely restricted to post-testicular region. Parasites of freshwater and marine fishes. Type genus *Homalometron* Stafford, 1904 (syn. *Anallocreadium* Simer, 1929). Includes also:

Microcreadium Simer, 1929.

Crassicutis Manter, 1936.

Myzotus Manter, 1940.

An unnamed genus reported by Manter (1941).

Deropristiinae subf. nov.

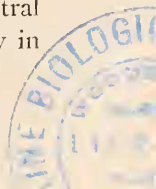
With characters of the family. Body elongate and spinose with enlarged spines on the middorsal and lateral regions of forebody. Genital pore median, anterior to ventral sucker; cirrus sac present. Cirrus and metraterm with prominent spines; genital sinus tubular. Ovary and anterior testis separated by a space into which the uterus may extend. Vitellaria scanty, between levels of cirrus sac and anterior testis. Parasites of migratory fishes; larval stages marine. Type and only genus *Deropristis* Odhner, 1905.

Since the subfamilies *Lepocreadiinae* and *Homalometrinae* differ chiefly in respect to the terminal genitalia, their validity may be questionable. However, differences in their cercariae and the fact that both subfamilies have become established in the literature probably justify their retention. Manter (1926) expressed the view that the genera *Anallocreadium* and *Homalometron* probably are synonymous. We can find no basis for maintaining the separate identity of these genera. Since *Homalometron* has clear priority, the name *Anallocreadium* is not available for the subfamily *Anallocreadiinae* proposed by Hunter and Bangham (1932). In restudying Stafford's collection, Miller (1941) has expressed the opinion that *Homalometron* and *Lepocreadium* may be synonymous. We have placed these genera in separate subfamilies and fail to see the reason for Miller's opinion since *Lepocreadium* has a long

excretory vesicle and cirrus sac while *Homalometron* has a short vesicle and lacks a cirrus sac. Incidental to the present study, we have determined that the excretory system of *H. pallidum* is very similar to that of *Deropristis*, the chief difference being a much larger number of flame cells in *Homalometron*, particularly in the anterior groups.

The trematodes assigned by various authors to the families Gyli-
auchenidae and Opistholebetidae present a perplexing problem which
Manter (1940) has discussed recently. Travassos (1934) and Ozaki
(1937) have assigned these families to the superfamily Paramphisto-
moidea, although they contain genera ranging from the usual distome
type to forms superficially resembling the amphistomes. Figuring largely
in this disposition was the presence of lymphatic vessels in certain genera.
Manter (1940) pointed out the resemblance of certain gyli-
auchenids to the Lepocreadiinae and Anallocreadiinae and described what appeared to
be lymph channels in species of *Opechona* and *Pseuclapidapedon*. On
the other hand, he cites Carassotrema, a gyli-
auchenid, which lacks lymphatic vessels, indicating that their presence does not necessarily denote
amphistome affinities. Manter therefore concluded that the family Gyli-
auchenidae probably should be considered in the superfamily Allo-
creadioidea.

A study of Ozaki's (1937) excellent descriptions of the gyli-
auchenids affords convincing evidence that they are aberrant forms closely related
to the family Lepocreadiidae. Their peculiar body shape can be ex-
plained by failure of the hindbody to grow during post-cercarial develop-
ment, with a compensating elongation of the forebody and a resultant
shifting of certain internal organs anteriorly. The so-called excretory
papilla then would correspond to the post-acetabular region of ordinary
distomes. Several morphological features support this explanation.
First, the genera *Petalocotyle*, *Telotrema*, *Flagellotrema* and *Gyli-
auchen* comprise a fairly complete series of body forms ranging from the usual
distome type to one resembling the amphistomes. In this series, there is
a progressive elongation of the prepharynx and decrease in the length
of the intestinal ceca until they are little longer than the pharynx in
*Gyli-
auchen*. There is also a progressive decrease in the length of the
excretory vesicle and retreat of the testes from the hindbody which be-
comes too small to contain them. Elongation of the forebody is sug-
gested not only by the length of the prepharynx, but also by the distance
separating flame cell groups near the middle of the body; the genital pore
and ventral sucker become widely separated. Furthermore, the lymph-
atic vessels which extend posteriorly only to the ventral sucker or about
one-fourth the body length in *Petalocotyle*, likewise reach the ventral
sucker in *Telotrema* but are consequently almost as long as the body in



this species. Progressive reduction of the hindbody is indicated not only by the shortening of the intestinal ceca and excretory vesicle, but also by the manner in which the flame cell groups are crowded in the hindbody of the intermediate form, *Telotrema*, and apparently become reduced in number in *Flagellotrema*.

The genital complex and excretory system of the gyliachenids agree well with those of the lepocreadiids and certainly are unlike those of typical amphistomes. In no case, is the ovary posterior to the testes as in most amphistomes and only in *Flagellotrema*, where it lies between the testes, does it approach the condition found in certain short-bodied amphistomes. The reduction and anterior displacement of the vitellaria may be correlated with the shortening of the intestinal ceca and compensating elongation of the prepharynx. The somewhat shortened ceca and arrangement of the reproductive system in the lepocreadiid *Opechonoidea* are suggestive of certain gyliachenids.

On the basis of structure, it could be argued that either the amphistome or the distome is the primitive gyliachenid body type. This question cannot be answered until the larval stages are discovered. In view of the fundamental morphological resemblances of the gyliachenids to the lepocreadiids, we believe that the family Gyliachenidae does not belong in the Paramphistomoidea but instead in a common superfamily with the Lepocreadiidae. Further study may in fact necessitate the combination of these families if it is shown, as some observations indicate, that the lymphatic system in trematodes is correlated with physiological requirements that may arise independently in various groups.

Secondary acquisition of amphistome characteristics in the family Opistholebetidae is suggested by the series *Maculifer*, *Heterolebes*, and *Opistholebes*. There is some suggestion that this group may be related to the Opecoelidae but the evidence is not sufficiently clear to postulate affinities. This is true also of the family Cephaloporidae.

It is uncertain whether the families Allocreadiidae (*sensu stricto*), Opecoelidae, Lepocreadiidae, Acanthocolpidae, and Gyliachenidae represent only one or more than one superfamily. Our knowledge of life histories and embryological development, particularly of marine forms, is still fragmentary and it is possible that in certain groups the few life histories known are of species having atypical larval stages such as have been described in other groups and would by themselves be misleading as a basis for judging relationships.

SUMMARY

The life history of *Deropristis inflata* has been demonstrated experimentally. The cercaria is a trichocercous form developing in simple

rediae in the marine snail, *Bittium alternatum*. It encysts in *Nereis virens* and the eel, *Anguilla rostrata* serves as the natural definitive host which becomes infected by eating annelids containing metacercariae.

The genus *Deropristis* and *Dihemistephanus sturionis* are excluded from the family Acanthocolpidae which is redefined to include for the first time the genera *Lepidauchen*, *Pleorchis*, and *Pseudolepidapedon*. The family Pleorchiidae thereby becomes invalid.

It is proposed that the family Allocreadiidae be restricted to include only forms known or believed likely to have ophthalmoxiphidiocercariae with main excretory tubules not reaching the cephalic region of the body before receiving secondary tubules. The Allocreadiidae and Acanthocolpidae are regarded as separate but closely related families.

The genus *Anallocreadium* is reduced to synonymy with *Homalometron* and the subfamily Anallocreadiinae is renamed Homalometrinae. The Lepocreadiinae, Homalometrinae, and new subfamily Deropristiinae are regarded as a distinct family, the Lepocreadiidae. The family Gyli-*au*chenidae is believed to be nearer the Lepocreadiidae than the Paramphistomoidea. Whether the Allocreadiidae, Acanthocolpidae, Opecoelidae, Lepocreadiidae and Gyli-*au*chenidae constitute only one or more than one superfamily is not apparent from the fragmentary knowledge of life histories and embryology.

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